

DISTRIBUTION, ECOLOGY, AND TAXONOMY OF
ERYTHRONIUM (LILIACEAE) IN THE
SIERRA NEVADA OF CALIFORNIA

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ABSTRACT

Five species of *Erythronium* occur in the Sierra Nevada of California. A new species, *E. pluriflorum*, endemic to the south-central portion of the range, is described and illustrated. *Erythronium pusaterii* is elevated to the rank of species from *E. grandiflorum* and represents the most southern occurrence of the genus for western North America. Distribution and habitat preferences are discussed, and a key for Sierran *Erythronium* is also provided.

Approximately 25 species of *Erythronium* range from southern Europe and temperate Asia to the Atlantic and Pacific coasts of North America (Willis 1973). The evolutionary relationships within the genus are not well understood. There appear to be two major groupings of species (perhaps corresponding to subgenera) which have not been formally recognized. One of these includes the eastern North American and Old World species, and the other includes the species of western North America. Of the 18 species in North America (Kartesz and Kartesz 1980), 13 species are recorded for California (Munz and Keck 1959; Munz 1968). The greatest species diversity for the genus occurs in the northwest portion of the California Floristic Province (Applegate 1935; Allen and Antos 1988).

The taxonomy of Sierran *Erythronium* has remained essentially unchanged since Applegate's 1935 monograph of western North American species, except for the addition of *E. grandiflorum* Pursh subsp. *pusaterii* described by Munz and Howell in 1964 (recognized herein as *E. pusaterii*). The major key division for west American *Erythronium* is based on presence/absence of mottled leaves. All Sierran *Erythronium* species are diploid, $n=12$, $2n=24$ (Cave 1970 and counts by the third author).

Distribution. The Sierra Nevada contains five species of *Erythronium* that are primarily restricted to this mountain range. Three species are rare and highly localized in distribution. *Erythronium multiscapoideum* (Kellogg) A. Nelson & P. B. Kennedy and *E. purpurascens* S. Watson are more wide-ranging species that venture northward into the southernmost extension of the Cascade Range in Shasta County. Alpine, Calaveras, Fresno, Inyo, Kern, and Mono counties lack a confirmed occurrence for the genus in the Sierra Nevada (Fig. 1).

The northern Sierra Nevada contains three *Erythronium* species. *Erythronium purpurascens* occupies montane habitats between 1200–2450 m from Shasta County south to Tuolumne County (floristic works attributing this species to the southern Sierra Nevada of Tulare County are erroneous). The other two species, *E. multiscapoideum* and *E. tuolumnense* Applegate, occupy foothill woodland habitats generally below 600 m. *Erythronium multiscapoideum* is the only Sierra Nevada species with mottled leaves. This species can propagate by producing new bulbs at the ends of long slender rhizomes. It is widely distributed, ranging from Shasta County south to Mariposa County, and often occurs on serpentine substrates. *Erythronium tuolumnense* is a localized, rare endemic of Tuolumne County. Although this species is also cited as occurring in Stanislaus County (Munz and Keck 1959), no herbarium specimens or populations are known from that county. Moreover, records at the California Natural Diversity Data Base, Department of Fish and Game, cite Tuolumne County for all of the known occurrences. Geographically, *E. tuolumnense* is located near the center of the Sierra Nevada (ca. 30 km west of Yosemite National Park). Populations occur primarily on north-facing slopes between 500–1160 m, mainly in *Quercus kelloggii*–*Pinus ponderosa* stands within the South Fork and Middle Fork of the Stanislaus River and North Fork of the Tuolumne River drainages. The majority of the populations occur on federal lands administered by the Stanislaus National Forest and are managed to conserve the species under Forest Service sensitive plant policy. The distance between the northern and southernmost populations is only 25 kilometers. Reproduction is largely vegetative by means of numerous closely spaced offsets that develop into additional bulbs (Applegate 1935), a feature rare in Californian *Erythronium*. *Erythronium tuolumnense* also has perianth segments with well developed saclike appendages. It appears to be a remarkable relictual species, confined now to “cold air drainage” microhabitats. Its relationship within the genus remains uncertain.

The two southern Sierran members of the genus are high montane, occurring between 2100–2840 m, and are very localized and rare. *Erythronium pluriflorum* (described herein) is endemic to Chiquito Ridge in the San Joaquin River watershed in Madera County, and

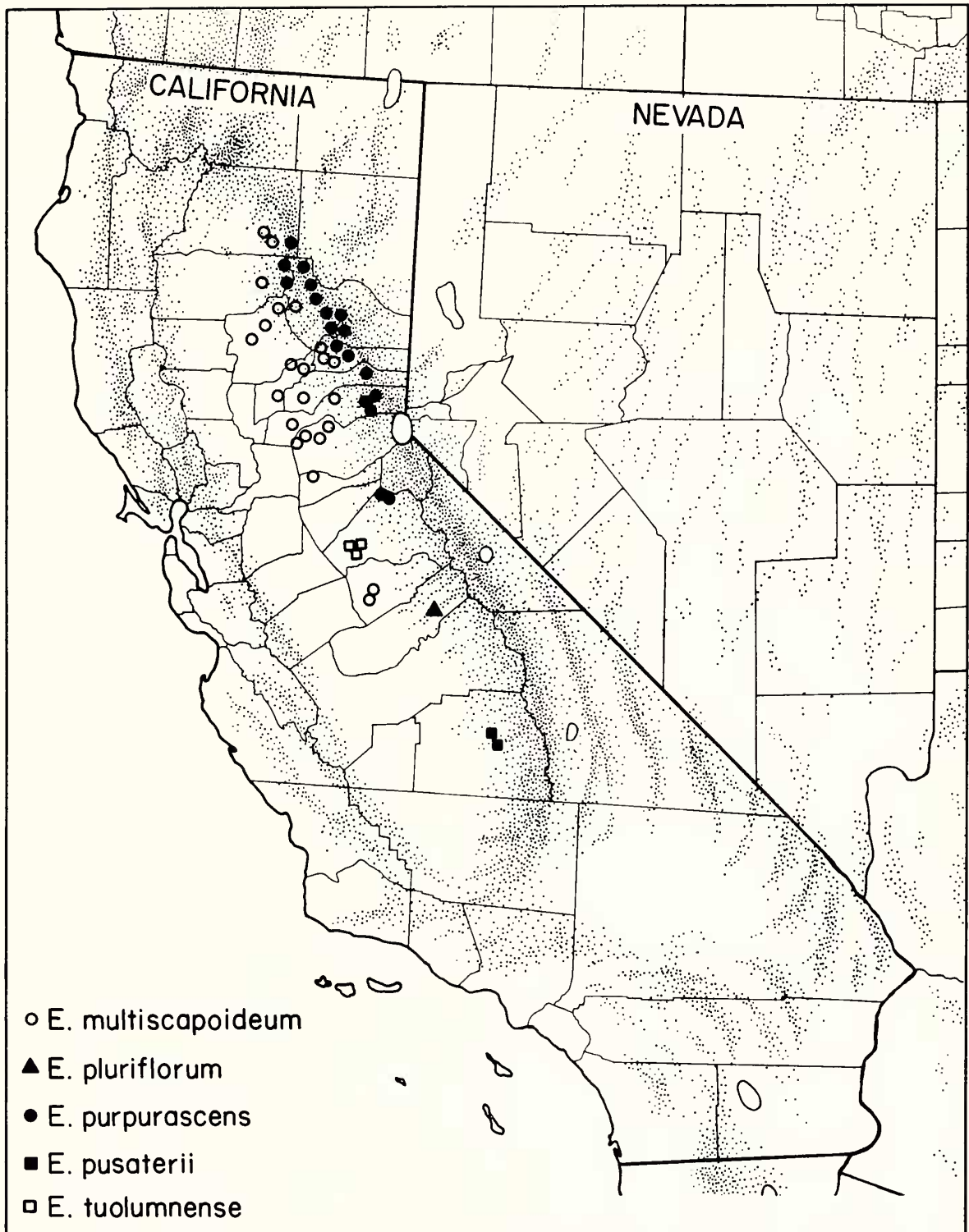


FIG. 1. Distribution of the genus *Erythronium* in the Sierra Nevada of California.

E. pusaterii is endemic to the Kaweah and Tule River watersheds in Tulare County (Shevock 1977). Given the number of field botanists who have collected in the Sierra Nevada this century, it is amazing that localized endemics are still being discovered and described at a relatively high rate (Shevock and Taylor 1987). This is of particular interest in regard to *E. pluriflorum*. This showy species is locally abundant within its restricted range, and road access to a large population has existed for many years.

KEY TO SIERRA NEVADA *ERYTHRONIUM*

- A. Leaves mottled; anthers cream-white; stigma plainly lobed, the lobes >1.0 mm long *E. multiscapoideum*
- A' Leaves not mottled; anthers usually yellow; stigma entire or with short lobes <1.0 mm long
 - B. Perianth segments bicolored, the terminal portion cream to white, the basal portion $\frac{1}{3}$ to $\frac{1}{2}$ bright yellow
 - C. Perianth segments 10–15 mm long, lacking saclike appendages at base *E. purpurascens*
 - C' Perianth segments 20–45 mm long, the inner three with saclike appendages at base *E. pusaterii*
 - B' Perianth segments bright yellow throughout
 - D. Perianth segments 25–35 mm long, 8–12 mm wide, the inner with appendages at base; style, stigma, and filaments \pm white *E. tuolumnense*
 - D' Perianth segments 15–28 mm long, 4–7 mm wide, lacking saclike appendages at base; style, stigma and filaments bright yellow *E. pluriflorum*

Erythronium pusaterii (Munz and J. T. Howell) Shevock, Bartel and Allen, stat. & comb. nov. (Fig. 2).—*Erythronium grandiflorum* Pursh subsp. *pusaterii* Munz and J. T. Howell. Leaflet. West. Bot. 10:104–105, 1964.—TYPE: USA, California, Tulare Co., along the South Fork Kaweah River below Hockett Lakes, Sequoia National Park, southern Sierra Nevada, 15 June 1964, 2560 m, Samuel J. Pusateri s.n. (holotype: RSA, isotype: CAS).

Bulb 5–7(–10) cm long, 1–3 cm wide. Leaves 2, unmottled, bright green with undulate margins, 20–30(–40) cm long, 3–5(–6) cm wide, oblanceolate to elliptic. Scapes 15–35(–45) cm tall, flowers, 1–5(–8), pedicels of unequal lengths. Perianth segments curved, acuminate to lanceolate, 20–45 mm long, bicolored, the terminal portion white, the basal $\frac{1}{3}$ – $\frac{1}{2}$ bright yellow, fading pinkish after anthesis, the inner three perianth segments with saclike appendages at base. Filaments and anthers yellow; stigma with three small lobes, <1 mm long. Capsule obovoid, 25–35 mm long, 10–15 mm wide; seeds brown, elliptical in outline, flattened. Chromosome number: $2n = 24$.

Exsiccatae. USA, California, Tulare Co., from the type locality, 20 Jun 1935, Dixon s.n. (UC); Jun 1963, Pusateri s.n. (RSA); 18 Jul 1980, Norris 100 (RSA, THRI); Moses Mountain, Jun–Jul 1895, C. A. Purpus 1341 (UC); Moses Mountain, Golden Trout Wilderness, Sequoia National Forest, T19S, R30E, Sect. 13, 8000–9000 ft, 30 Jun 1979, Shevock 6282 and 6286 (CAS); 13 Jul 1979, Shevock 6336 and 6351a (CAS); 23 Jul 1982, Shevock 9952 (CAS, RSA); 9 Jun 1984, MacFarlane s.n. (CAS); 4 Jul 1982, Holmes s.n. (DAV); Jordan Peak, Sequoia National Forest, T20S, R31E, Sect. 15, 9100 ft, 29 Jun 1976, Shevock 5133 (CAS, RSA); 14 Jun 1977, Shevock 5530 (CAS, RSA, UC); 15 Jul 1982, Shevock 9902 (CAS, FSC, RSA); Slate Mountain, $\frac{1}{2}$ mi SW of Quaker Camp, Sequoia National Forest, T21S, R32E, Sect. 18, 7300 ft, 1 Jul 1982, Shevock 9841 (CAS, FSC,

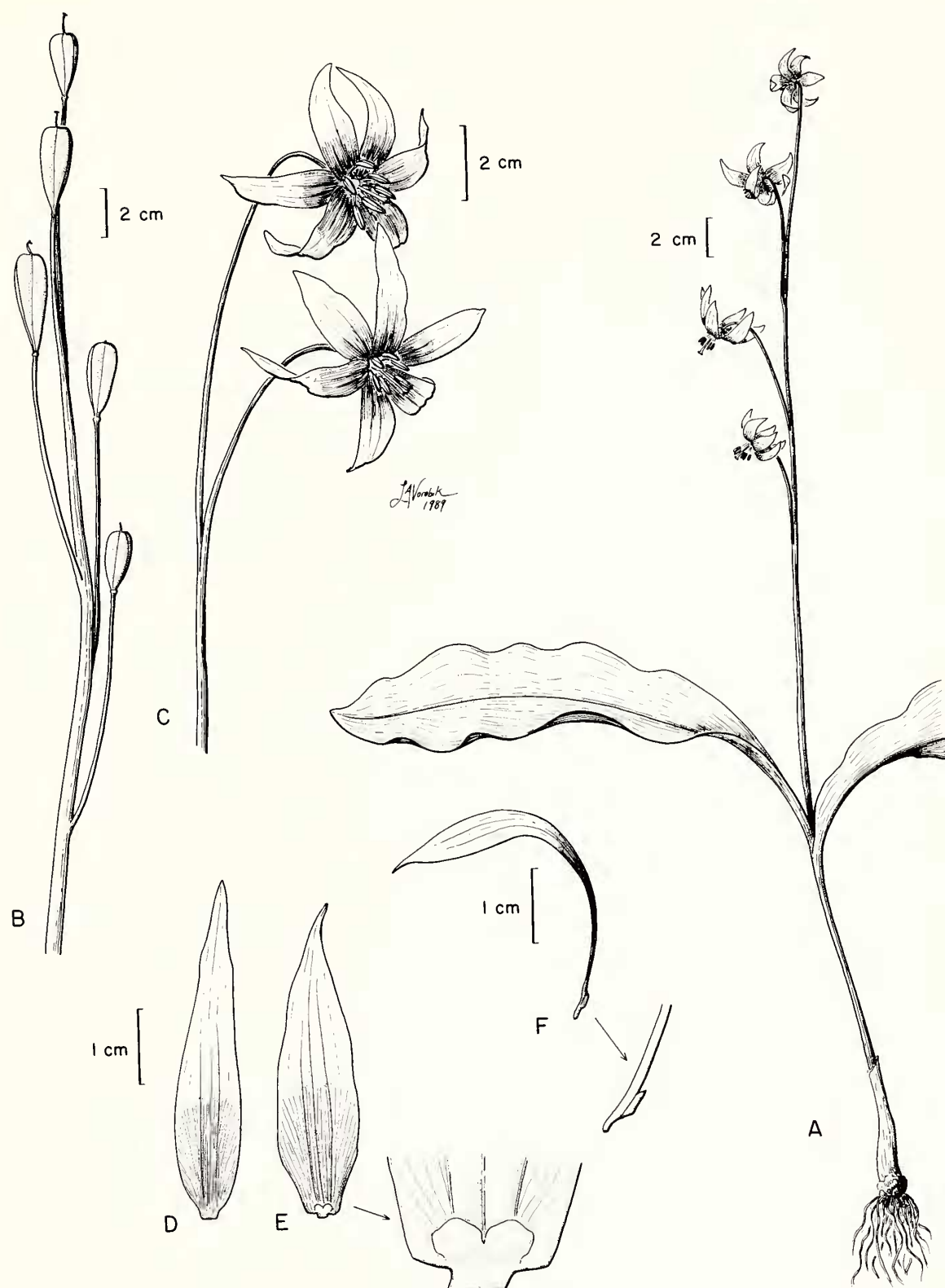


FIG. 2. *Erythronium pusaterii*. A, flowering scape; B, fruiting scape; C, close-up of flowers; D, outer perianth segment; E, inner perianth segment with saclike appendages; F, side view of perianth segment.

RSA); Slate Mountain at head of Bear Creek, T21S, R31E, Sect. 13, 8650 ft, 6 Jul 1982, Shevock 9845 (CAS, RSA, UC).

History of the Kaweah fawn lily. Samuel J. Pusateri was an instructor at College of the Sequoias, Visalia (Tulare County). He published the *Flora of our Sierran National Parks* in 1963. That

same year Pusateri sent to Philip Munz a photograph and a plant fragment of *Erythronium* collected along the Kaweah River near Hockett Lakes. Additional plant specimens were obtained the following year and were sent to Munz and John Thomas Howell. The Pusateri collection was obtained in June, and the description was published in September of the same year. When Munz and Howell described the “Kaweah fawn lily” in 1964, they only had two sheets of the plant along with some color transparencies. Neither Munz nor Howell had previously worked with *Erythronium*, nor were they able to observe this species in the field. Nonetheless, they correctly realized that the *Erythronium* from the South Fork of the Kaweah River was indeed a new entity.

Correspondence between Munz and Howell (attached to the isotype at CAS) indicates that their decision to include the Pusateri collection in *Erythronium grandiflorum* was based primarily on three characters: large flowers, saclike appendages at base of perianth segments, and unmottled green leaves. However, Munz and Howell (1964) noted that the range of the Tulare County material was remote from that of other forms of *E. grandiflorum*; the nearest populations of the latter are in the Yolla Bolla Mountains in Trinity County. Howell states in his letter to Philip Munz dated 30 July 1964:

“Sam Pusateri sent me two leaves and four flowers, so that I don’t have much to go on—but this material with his photos would seem to place the plant within the variation in *E. grandiflorum*. Sam has pressed the flowers so flat I am not sure if the inner segments have ‘basal appendages’ Applegate describes for the species, but I do find some flattened folds that may be remnants of these. If the appendages are present then I can see the Sierran plant only as a color variant of *E. grandiflorum* near *E. g. var. pallidum* (on account of unequal stamens). The undulate leaves are striking but can one be sure from herbarium material whether this is a noteworthy character? At the moment it seems like a variety of *grandiflorum*—but that feeling may come only from a lack of knowledge (which might come only from seeing a living plant).—Liliaceae are not easy!”.

A response from Munz (also attached to the CAS isotype) dated 7 August 1964 stated:

“On further study I agree with you about the status of Sam Pusateri’s *Erythronium* and I send you herewith a write-up hoping you can use it in the next Leaflets”.

During a review of the genus *Erythronium* for the Jepson Manual Project, the third author recognized that the Kaweah fawn lily did not belong with *E. grandiflorum*. The first author independently came to the same conclusion based on extensive observations of the plant in the field from the four known localities. Review of the

herbarium record shows that Purpus made the first collection of *E. pusaterii* in the summer of 1895. His specimen, labelled *E. purpurascens*, is the sole collection responsible for this species being cited for Tulare County in the southern Sierra Nevada (Smiley 1921; Jepson 1923; Applegate 1935; Munz and Keck 1959). *Erythronium pusaterii* was also collected by Dixon in 1935 (along the South Fork of the Kaweah River), but again, the significance of the specimen was not realized. It too was labelled *E. purpurascens*.

Distribution, habitat and phenology. *Erythronium pusaterii* occurs on rocky granitic or metamorphic outcrops primarily in subalpine coniferous forests of *Abies magnifica*, *Pinus murrayana* and/or *P. monticola* from 2225–2835 m. Plants form large colonies in areas where soil and humus accumulate, especially along fissures and ledges. This species is known from four localities comprising several distinct populations ranging from a few thousand individuals to several million. Flowering occurs shortly after or during snowmelt and extends from late May to mid July depending on the depth and duration of the snowpack. The distance between the northern and southernmost populations is 28 kilometers.

Relationships. In our view, *Erythronium pusaterii* is most closely related to the more widely distributed *E. purpurascens*, which it closely resembles except for its much larger size and the presence of saclike appendages on the inner perianth segments. Both species are high montane with several bicolored flowers per scape, and the flowers are very similar in color. The perianth segments of *E. pusaterii* are generally two to three times as large as those of *E. purpurascens*. *Erythronium purpurascens*, described by Sereno Watson in 1877, was the only montane species recorded for the Sierra Nevada at the time of the Purpus collection in 1895. Applegate (1935), who prepared a monograph of *Erythronium* in western North America, cited the Purpus collection as belonging to *E. purpurascens*. Although he had observed and collected every species discussed in his monographic treatment, he had not observed live material from the southern Sierra Nevada, and thus did not recognize the significance of this solitary and disjunct collection.

The similarities between *E. pusaterii* and *E. grandiflorum* noted by Munz and Howell (large flowers, saclike appendages on the perianth, and unmottled leaves) are found in a number of western North American species, and do not characterize *E. pusaterii* and *E. grandiflorum* alone. *Erythronium pusaterii* is distinguished from *E. grandiflorum* by its bicolored, more numerous flowers (ranging up to 8 per scape); entire to short-lobed stigma; and shorter style, filaments, and anthers. *Erythronium grandiflorum* throughout its range has perianth segments that are golden yellow, lighter near the base (Applegate 1935), and anther color varying from cream to yellow or dark red. Various varieties and subspecies based on anther color

have been described; however, this criterion has proved to be of limited taxonomic value. Major floristic manuals within the range of this species do not recognize these infraspecific taxa (Cronquist et al. 1977; Hitchcock et al. 1969), and we concur with this interpretation.

Rarity status. *Erythronium pusaterii* has a highly restricted geographic range, occurring at only four locations in the upper Kaweah and Tule River watersheds. All populations are free from human disturbances at present. The South Fork Kaweah River populations are within Sequoia National Park where the species is adequately protected. Moses Mountain, the location of the largest numbers and concentrations of the Kaweah fawn lily, is within the Golden Trout Wilderness, Sequoia National Forest and is likewise protected. The populations within Sequoia National Forest on Jordan Peak and Slate Mountain are managed to conserve the species under Forest Service sensitive plant policy. The localized nature of the species distribution and level of field work conducted by the first author in the general area suggest that additional occurrences are unlikely to expand the range of this endemic species of the southern Sierra Nevada.

Erythronium pluriflorum Shevock, Bartel and Allen, sp. nov. (Fig. 3)—TYPE: USA, California, Madera Co., Chiquito Ridge along the N and NE slope of Shuteye Peak on granitic rocky slopes, subalpine coniferous forest, Sierra National Forest, T7S, R23E, Sect. 2 N½, 8250 ft, 25 May 1989, *Shevock, Bartel, and Allen 11854* (holotype, CAS; isotypes, FSC, MO, NY, RSA, UC, US, UVIC).

Folia 7–40 cm longa elliptica vel oblanceolata non maculata; scapus floribus plerumque pluribus; flores tepalis 15–28 mm longis late lanceolatis recurvis luteis aetate subaeneis, sine appendiculis saccatis basalibus; antheris luteis, filamentis luteis tenuibus; stylo clavato luteo, stigmatе integro vel brevilobato, lobi minus quam 1 mm longis.

Bulb 5–7(–9) cm long, 1–2 cm wide. Leaves 2 (rarely 3), unmottled, bright green with undulate margins, 7–35(–40) cm long, 1.5–4.5(–6) cm wide, oblanceolate to elliptic. Scapes 7–35(–45) cm tall; flowers, 1–10(–21), nodding, pedicels of unequal lengths. Perianth segments recurved, elliptic to lanceolate, 15–28 mm long, 4–7 mm wide, bright yellow fading bronze to pinkish after anthesis, saclike basal appendages lacking. Filaments bright yellow, slender, the inner ones longer; anthers bright yellow, when dehiscent approximately ½ as long as the filaments; style bright yellow, clavate, stigma entire or with very short lobes (<1.0 mm). Pedicels elongating markedly after anthesis, erect, up to 12.5 cm long. Capsule obovoid, 25–35 mm

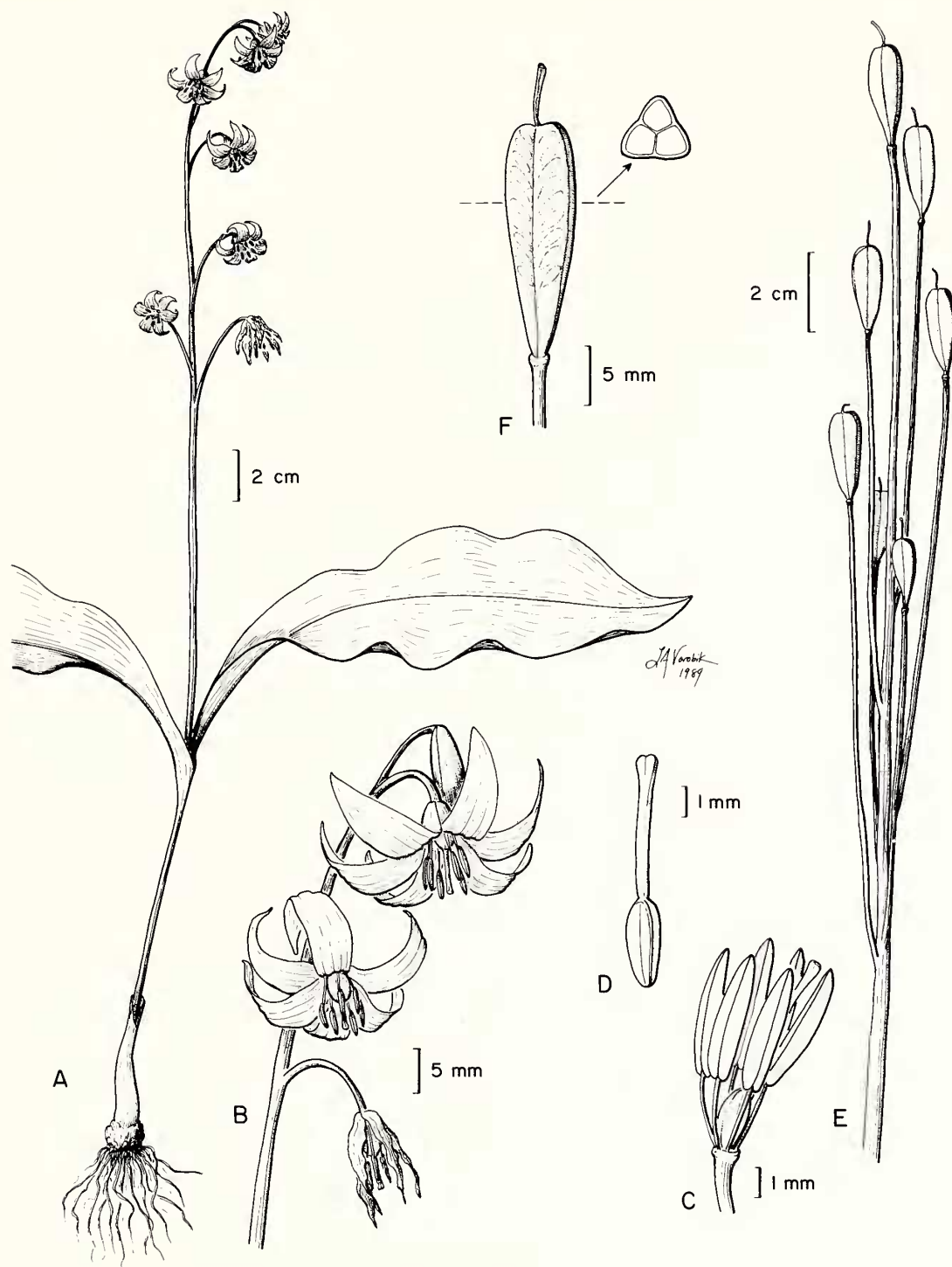


FIG. 3. *Erythronium pluriflorum*. A, habit; B, close-up of flowers; C, stamens; D, stigma; E, fruiting scape; F, capsule.

long, 6–10 mm wide. Seeds brown, narrowly elliptical in outline, flattened. Chromosome number: $2n=24$.

Paratypes. USA, California, Madera Co., type locality, 22 Aug 1907, *J. Murdoch Jr.* 554 (CAS [not located], GH!, NY!, US!) 23 Jun 1984, *MacFarlane s.n.* (CAS); 1 Jun 1988, *J. Clines* 148 (CAS), 29 Jun 1988, *Clines and Lorenzana* 158 (CAS, FSC); 2 Jul 1988, *Shevock and Bartel* 11844 (CAS, FSC, RSA, UC); Little Shuteye

Peak, T6S, R23E, Sect. 20 & 21, 7600–8300 ft, 13 Jun 1989, *Shevock 11857* (CAS, FSC, MO, NY, RM, RSA, UC, US, UVIC); road adjacent to Chilkoot Lake, T6S, R23E, Sect. 17 NW¼ NW¼, 7300 ft, 13 Jun 1989, *Shevock 11858* (CAS, RSA); rock outcrops ¼ mi S of Shuteye Pass, T7S, R23E, Sect. 12 NW¼, 7600 ft, 14 Jun 1989, *Shevock 11873* (CAS, FSC, MO, NY, RSA, UC, US, UVIC).

This distinctive, beautiful, many-flowered *Erythronium* was first brought to our attention by Joanna Clines, a seasonal employee hired by the Sierra National Forest in 1988 to do botanical surveys of rare species. A subsequent search of *Erythronium* collections at CAS, DAV, DS, FSC, JEPS, POM, RSA, and UC revealed one specimen collected by J. Murdoch Jr. in August 1907 that represents the first collection for this new species. This specimen was filed for 81 years among specimens of *E. purpurascens*. Both Applegate (1935) and Smiley (1921) cited the Murdoch collection as *E. purpurascens*. Roger MacFarlane, a Research Associate at CAS and student of Liliaceae, has recently studied selected members of *Erythronium*. He independently recognized that the Murdoch collection from “Shuteye Mountain” in Madera County did not represent *E. purpurascens*. Collections and photographs were obtained by MacFarlane on 23 June 1984. He correctly concluded that the Shuteye Peak plants were new to science (pers. comm.) but he did not formally describe the new species.

Distribution, habitat and phenology. *Erythronium pluriflorum* grows on rocky granitic slopes in a very open *Pinus monticola*–*Abies magnifica* forest from 2100–2700 m. Plants form large colonies in bedrock crevices and ledges where soil and humus accumulate. Flowering extends from mid-May to mid-July depending on snowpack duration and temperature. The Murdoch collection obtained in August 1907 represents the extreme range of flowering season, corresponding to an exceptionally heavy snowpack in the winter of 1906–1907 (Hill 1975:40). *Erythronium pluriflorum* is known from a few scattered populations along Chiquito Ridge from Chilkoot Lake and Little Shuteye Peak southward to Shuteye Peak and Shuteye Pass, San Joaquin River watershed, Sierra National Forest. Both the Shuteye Peak and Little Shuteye Peak populations number in the millions of individuals. Associated species include *Lomatium torreyi* (J. Coulter & Rose) J. Coulter & Rose, *Penstemon newberryi* A. Gray, *Saxifraga bryophora* A. Gray, *Sedum obtusatum* A. Gray subsp. *obtusatum*, *Sorbus californica* E. Greene, and *Triteleia dudleyi* Hoover.

Relationships. *Erythronium pluriflorum* most closely resembles *E. purpurascens* and *E. pusaterii*. All three species produce large numbers of flowers, commonly up to 8 per scape; which exceeds the 1–4 flowers per scape produced by the majority of *Erythronium* species. A unique feature for *E. pluriflorum* is the presence of two separate

phases of flower production on mature/robust individuals. Initially, each scape develops up to 8 flowers including the terminal flower for the raceme. The second flowering phase appears to be delayed until anthesis and pedicel elongation of the first phase. The second flowering phase is somewhat congested midway on the scape and the flowers are slightly smaller. These mature individuals can produce up to 21 flowers per scape. We are unaware of this flowering pattern occurring in any other species of *Erythronium*.

The single collection of *E. pluriflorum* known to Applegate (1935) and Smiley (1921) was placed within *E. purpurascens*, which is probably its nearest relative. Faded specimens of *E. purpurascens* and *E. pluriflorum* could be confused in herbaria, though they are easily distinguished in the field by tepal color. Other characteristics such as the larger leaves, and color of style and filaments also help to separate *E. pluriflorum* and *E. purpurascens*. The flowers of *E. pluriflorum* are bright yellow throughout and turn bronze to pinkish after anthesis while the flowers of *E. purpurascens* are white with a yellow base and become purple tinged with age. The leaves of *E. pluriflorum* and *E. pusaterii* are very similar in size, color, and appearance with undulate margins. Plant height is often similar as well. The species differ in flower size and color; those of *E. pusaterii* are nearly twice as large, with the terminal portions of the tepals white.

Both *E. pluriflorum* and *E. pusaterii* occur in soil pockets of high montane rocky summits. Although *E. purpurascens* occurs further north, its preferred habitat has similarities to those of these two species. Sites that appear to be suitable habitat for either *E. pluriflorum* or *E. pusaterii* occur within the 120 km that separate these two species (within Fresno County), but the deep canyons of the Kings and San Joaquin Rivers have probably served as major barriers for colonization of these habitats.

Rarity status. Although *Erythronium pluriflorum* is relatively abundant along Chiquito Ridge, this species is entirely limited to this locality comprising an area less than 0.5 km by 11 km. From a phytogeographical perspective, this is an extremely narrow montane endemic. Since this high elevation species has very specific growing conditions, the success in cultivation at low elevations is unlikely, and therefore it should not be collected for this purpose. None of the populations occur in any protected area; however, the Sierra National Forest will manage and conserve this species under Forest Service policy via their sensitive plant program.

Conclusion. We believe that all three endemic species of *Erythronium* in the Sierra Nevada are relictual taxa isolated from interaction with the remainder of the genus. Both *E. pluriflorum* and *E. pusaterii* are locally abundant, but extremely restricted in geographic range. Together with the more widespread *E. purpurascens*, they may be

relictual remnants of an ancestor that was once more widely distributed. The likelihood of extending the range for *E. tuolumnense*, *E. pluriflorum* and *E. pusaterii* appears to be remote. The extent of past glaciation in the Sierra Nevada is probably not so important to the distribution of *Erythronium* species as the subsequent shift to a warmer and drier climate, leading to a reduction and fragmentation of suitable habitat. The north-south orientation of the Sierra Nevada coupled with increasing elevational relief, narrowing width and increasing aridity as one proceeds southward may also aid in explaining the disjunct nature of *Erythronium* species in this mountain range. Most western North American *Erythronium* species are allopatric, and hybridization can occur in areas of sympatry (Applegate 1935; Allen and Antos 1988). However, natural hybridization between Sierran *Erythronium* species is lacking due to geographic isolation and other ecological/habitat parameters.

ACKNOWLEDGMENTS

We thank Joanna Clines for the *Erythronium* collection that provided the catalyst for this paper and John Lorenzana of the Sierra National Forest for assistance, photographs and field notes. The assistance of Roger MacFarlane, for making his data accessible to the authors is also greatly appreciated. We are grateful to the curators of GH, NY, and US for loan of specimens. Special thanks to Linda Vorobik from the Jepson Herbarium for providing the excellent botanical illustrations. We also thank Wayne Ferren, Rodney Myatt, and Dale McNeal for providing ways to make this paper more informative.

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(Received 30 Nov 1989; revision accepted 22 May 1990.)

ANNOUNCEMENT

AWARDS FOR BEST PAPERS: CALIFORNIA BOTANICAL SOCIETY THIRTEENTH GRADUATE STUDENT MEETINGS

Completed Research (\$100)

AARON LISTON, Department of Genetics, University of California, Davis—Evidence for rapid allopatric speciation in *Astragalus* section *Leptocarpi* subsection *Californici*

Research in Progress (\$100)

CLAUDIA M. TYLER, Department of Biological Sciences, University of California, Santa Barbara—Factors affecting seedling establishment in chaparral after fires.

Proposed Research (tie, \$50 each)

RANDY K. ZEBELL, Department of Biological Sciences, San Francisco State University, San Francisco—A biosystematic investigation of variation in *Calochortus venustus*

MAILE C. NEEL, Department of Biological Sciences, University of California, Santa Barbara—Morphological and allozyme variation in *Echinocereus engelmannii* var. *munzii*